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Nest size, nest building behaviour and breeding success in a species with nest reuse: the white stork *Ciconia ciconia*

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Nest size and nest building behaviour affect individual fitness and thus, selection may act on these traits. Most data on nesting behaviour come from species that build a nest for each new breeding attempt, whereas almost nothing is known regarding nest reusers. Here, the association between nest size and nest building behaviour, and occupation date as well as breeding success of the white stork *Ciconia ciconia*, a migratory species with nest reuse, is presented. Large nests were occupied earlier and showed higher breeding success, even accounting for the confounding effect of the breeder's age. In addition, nest size increased steadily over the entire breeding season and only ceased when reproduction failed. However, this increase was not related to breeding success variables. Finally, nest size was related to the number of times that it was used in the past and thus, to the probability of successful reproduction. These results suggest that storks may seek and compete for bigger nests and that nest size could be an indicator of individual and/or nest-site quality.

Introduction

Many animals build structures for protecting and raising their offspring during reproduction, which are usually called nests (Hansell 2005). There is huge variability between species in the way that nests are constructed and maintained as well as in nest characteristics, such as size, shape, composition or location. Even within species, variability in nest characteristics is noteworthy, which reinforces the idea that nest characteristics are strongly dependent on individual behaviour and ability (Collias & Collias 1984, Moreno *et al*. 1994, 1995). Such patent variability may be the reason for the wide array of hypotheses proposed to explain intraspecific variability in parameters such as nest size and nest building behaviour (Møller 1990, Moreno *et al*. 1994, Soler *et al*. 1995, 1996, 2001, Palomino *et al*. 1998, López-Iborra *et al*. 2004, Lamber & Kleindorfer 2006, Wiebe *et al*. 2007).

Most studies regarding nest-building behaviour and the role of nest characteristics have focused on species that build a new nest for each breeding attempt, whereas little is known about nidicolous species that reuse nests over several breeding seasons, such as raptors (Roulin *et al*. 1997, Margalida & Bertran 2000, Lohmus 2003, Margalida *et al*. 2007) or storks (Tortosa & Villafuerte 1999). However, one could expect that selective pressures have evolved differently under each strategy and, consequently, findings for "nest builders" may not be fully applicable for "nest reusers" species. For instance, nest characteristics and/or building behaviour have been shown to be an index of individual quality in some "nest builders" species (Fargallo *et al*. 2001, 2004, Tomas *et al*. 2006, Moreno *et al*. 2008), but it is difficult to conceive the same kind of association in "nest reusers" because the current owner seldom builds the nest.

The white stork, *Ciconia ciconia*, is potentially an excellent model to study the role of nest characteristics and nest building behaviour in a nest reuser species. This species builds large, open and perennial nests on wide array of supports (e.g. trees, cliffs, pylons, roofs, chimneys; Cramp & Simmons 1977, Tryjanowski *et al*. 2009) that are reused for years or even decades (Cramp & Simmons 1977, Barbraud *et al*. 1999, Prieto 2002, Vergara *et al*. 2006). Current breeders do not usually build the nest, but they repair and add new material to a pre-existing nest (Cramp & Simmons 1977). The construction of new nests is often associated with increasing populations, where new recruited pairs must suit and arrange a new nesting site (Vergara *et al*. 2007a). This phenomenon generally takes place late in the breeding season, when most available old nests are already occupied. Then, young inexperienced pairs, which are breeding for the first time, begin nest building (Prieto 2002). Although males take charge of carrying most of the material for repairing a nest or constructing a new one, females are also involved in the process (Schulz 1998). The carrying of material to the nest begins with the first returned bird of each pair (usually the male; Barbraud *et al*. 1999, Barbraud & Barbraud 1999), but the addition of material continues throughout the breeding period even after the young have fledged (Cramp & Simmons 1977).

The role of nest characteristics and nest building behaviour has been poorly explored in this species. Some studies suggest that larger nests are occupied earlier and show higher breeding success than smaller ones (Tortosa & Redondo 1992, Bocheński & Jerzak 2006, Tryjanowski *et al*. 2009). However, an important confounding factor, such as the individual's age, was not accounted for and consequently it is impossible to determine to what extent success differences among nests were a result of nest characteristics or just a matter of the occupant's phenotypic quality. In addition, Prieto (2002) proposed permanent competition for nest occupancy among white stork pairs during each breeding season. Despite nest-site fidelity (Vergara *et al*. 2006), nests do not have an owner at the beginning of the breeding season and occupancy turnover is common prior to definitive settling of the pair (Wuczyński 2005; authors' unpubl. data). The definitive pair is usually the same as the one in the previous year (Bocheński & Jerzak 2006), but it must win and actively defend the nest against competitors each breeding season (Prieto 2002). Moreover, fights among individuals, material theft and even clutch destruction are usually observed in white stork colonies (Tortosa & Redondo 1992, Prieto 2002). Furthermore, individuals arrive earlier in denser populations (Gordo *et al*. 2007), which also suggests competition for nests. In summary, there is evidence that suggests the occurrence of nest competition in the white stork, especially amongst individuals in colonies. In this situation, one could expect a despotic distribution, with individuals of best phenotypic quality occupying the best nest-sites (Serrano & Tella 2007). In the white stork, individual quality is related to ageing and gaining of experience (Vergara & Aguirre 2006, Nevoux *et al*. 2008), and this may explain why older individuals generally occupy most favourable positions in the centre of colonies, while younger individuals are relegated to the periphery (Vergara & Aguirre 2006).

The aim of the present study is to explore the relationship between nest size, occupation date and breeding success in a long-term marked population of white storks breeding in a colony at high density. If nest size confers fitness differences to its occupants (Sasvari *et al*. 1999, Tryjanowski *et al*. 2005), we expect larger nests to be occupied earlier and by individuals of best phenotypic quality or by more experienced individuals. Furthermore, nest-building behaviour during the entire breeding season was studied with the aim to determine if material contribution is associated with breeding success once pairs are settled.

Material and methods

Study area and general methods

The studied colony is located in central Spain (Madrid province, 40.7°N–3.8°E) in a "*dehesa*" of ashes (*Fraxinus* spp.), a traditional countryside landscape in which wood exploitation, livestock raising, and crop cultivation share the same area. The colony has increased from one nest in 1989 to more than 170 nests at present (Vergara *et al*. 2007a). Most nests are located on the trunks of loped ashes (where they are easily accessible, average distance from the ground = 3.2 m) with few nests on branches of ashes or oaks (< 10%), and are spread over an area of 10.8 ha (average distance between pairs to nearest nests = 25.8 m). Since 1999, an exhaustive monitoring of reproduction of all breeding pairs of the colony has been conducted. Therefore, we know the number of years that each nest was occupied during the period 1999–2008 (not all nests were occupied every year). The number of these years ranged from one to nine or more (for those nests built before 1999).

Nest occupation, breeder age and breeding success

During the 2007 and 2008 breeding seasons, the colony was visited once a week starting from the end of November (of 2006 and 2007, respectively) to determine *nest occupation date*. Nest occupation date was defined as the first day that an individual was sighted perching, defending or constructing a certain nest (Vergara *et al*. 2007b). Due to some turnover of individuals in nests at the beginning of the breeding season, the final occupant was not always the first individual to arrive at the nest (Wuczyński 2005, author's unpubl. data). If we assume that better nest-sites are the first to be occupied (Newton 2004, Tryjanowski *et al*. 2005, Sergio *et al*. 2007), occupation date of the first nest is indeed a better surrogate of nest quality than the arrival date of breeders to a certain nest. Prior to laying date, individuals breeding at each nest were identified by reading codes from PVC rings with a telescope whenever possible (not all individuals were banded). The exact age of an individual was derived from the ring codes, since all birds from the colony were banded as nestlings. Individual age was used as a measure of quality because breeding success (Vergara & Aguirre 2006, Vergara *et al*. 2007b, Nevoux *et al*. 2008) and survival (Schaub *et al*. 2005) are related to age in the white stork. In those cases with both members of a pair marked, we used the average age of the pair to avoid pseudoreplication in the breeding data.

Weekly visits to the colony from the end of March onwards provided data on breeding success of the pairs. Several variables were defined:

1. *Laying outcome*: a binomial variable to codify the presence or absence of clutches in occupied nests. Nest predation was low (< 4%) and early abandonment is rare in our population (Aguirre & Vergara 2009). Hence, false absences are highly improbable. Nevertheless, preyed upon (2) and deserted (4) nests found during the two study years were excluded from the analyses.
2. *Clutch size*: number of eggs laid, excluding zeros (mean = 4.4, SD = 0.7, range 3–6).
3. *Productivity*: number of chicks 40 days after hatching, excluding zeros (mean = 2.5, SD = 0.9, range 1–5). This is an accurate measure of the final number of fledglings (fledging age around 60 days) due to low mortality during the latter stages of chick development (Andrzejewska *et al*. 2004).
4. *Breeding outcome*: a binomial variable to codify successful (at least one nestling 40 days after hatching) and failed (no chicks) nests in which eggs were laid.

The reason for which a pair fails to breed (e.g. predation, accident, death of a parent, etc.)

or breed successfully is different from the reason for which a pair produces one, two or three eggs/chicks (e.g. parental quality). Therefore, each type of variable (binomial or continuous) provides a different perspective for the same biological phenomena.

Nest size measurements

Nest size was estimated from three measurements: length (mean = 180, range 60–300 cm), width (mean = 150, range 50–240) and height (mean = 60, range 20–140 cm). Length was the longest measurement on the nest surface, while width was the measurement of its corresponding perpendicular axis. Height was measured at three equidistant points on the nest border and averaged to obtain a more accurate measurement. Two new variables were calculated from these measurements: nest area [$\pi \times$ (length/2) × (width/2)] and nest volume (height × area) (see also Kosicki *et al*. 2007). As expected, nest area and volume were strongly correlated (e.g. initial measurements in 2007: $r = 0.77$, $F_{1,146} = 213.47$, $p < 0.001$). To avoid the possible error of variance inflation due to the strong collinearity of these two variables (Quinn & Keough 2002), models including only one of the variables of nest size as a predictor (*see* Statistical analyses) were used. We used Akaike's Information Criterion (AIC; Akaike 1973) to determine the best predictor (i.e., the model including nest area and the model including nest volume). Nest area showed the lowest AIC in all cases (results not shown). For this reason we decided to use only nest area as a measure of nest size throughout this study. Nevertheless, in no case did the use of nest area or nest volume modify the significance of the results.

Nest size was measured prior to the arrival of individuals (November), just after the last laid egg (around April; variable according to the laying phenology of each pair), and after fledging of all chicks (July). These measures were designated as initial, medium and final, respectively. The aim of the three measures performed in the breeding seasons of 2007 and 2008 was to more accurately study nest-building behaviour of storks through the breeding season and its possible role as a pre- or post-mating signal. Occupied nests without clutches (laying outcome = 0) were measured in the last week of April. Differences for each nest size measurement were calculated as: (1) medium – initial and (2) final – medium.

Statistical analyses

We tested for the effect of nest size (continuous predictor variable) on nest occupation and breeding success by means of General Linear Mixed Models (GLMM; for occupation date, clutch size and productivity) or Generalized Linear Mixed Models (GLIMMIX; for laying outcome and breeding outcome) with a binomial error distribution (Littell *et al*. 1996). All mixed models included year as fixed and nest as a random factor to avoid pseudoreplication (Hurlbert 1984). In the models for breeding outcome and productivity, clutch size was included as a covariate. In the nest occupation, clutch size and productivity models, age was included as a covariate to control for its confounding effect on arrival date and breeding success (i.e., older individuals arrive earlier and have higher breeding success; Aguirre & Vergara 2007, Vergara *et al*. 2007b). Since almost no marked individual failed during reproduction, models for laying and breeding outcome could not be run by including age as a covariate (i.e., there were not enough zeros). New nests built in 2007 and 2008 were not included in the within-year change analyses, nor in the study of the associations with breeding success variables because these nests did not have initial measurements. The low sample size for new nests (n = 13) did not allow for an independent analysis.

Changes in nest size during the two breeding seasons (2007 and 2008) were assessed by means of a repeated-measures ANOVA using nest area as a dependent variable in the initial, medium and final measures. Only successful nests (at least one chick fledged) were included in this analysis. Year was included as a fixed factor to test for possible differences between years in growing rate. To avoid pseudoreplication, we randomly selected measurements from one year (2007 or 2008) for those nests with initial, medium and final measures in both years. The assumption of circularity in the variance-covariance matrix

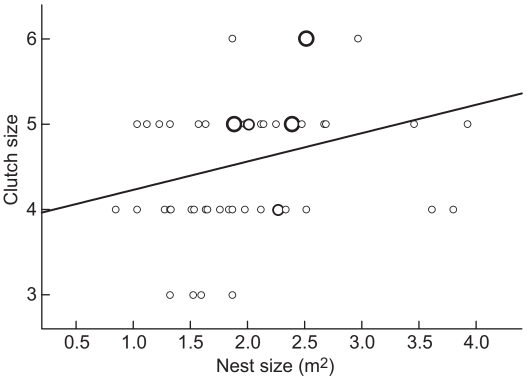

Fig. 1. Clutch size *versus* nest size at the beginning of the breeding season. The line represents the best fitted linear regression. Overlapping points are represented by differently sized symbols (smallest to largest, 1, 2 and 3).

was assessed by the Greenhouse-Geisser and Huynh-Feldt epsilons (ε_{GG} and ε_{HF}) for compound symmetry (von Ende 1993). Epsilons were used to calculate adjusted estimates of the degrees of freedom and p values for F statistics of models according to the severity of the violation of the assumption of circularity.

To check the hypothetical signalling function of nest size changes during the breeding season, four mixed models were performed between changes in nest size and breeding parameters. The difference between the initial and medium measures was used as a predictor of laying probability and clutch size. The difference between medium and final measures was used as a predictor of productivity and breeding outcome. Models for breeding outcome and productivity also included clutch size as a covariate. Whenever possible (*see* above) we included breeder age as a covariate to control for its potential confounding effect.

Finally, the association between the number of occupation years and nest size (on initial measure of 2008) was assessed by a single regression between both variables.

Sample sizes varied among models (*see* Results) because we were unable to measure all variables (nest occupation date, breeding success variables, breeder's age and nest size) in all the nests. All analyses were performed with the SAS statistical software (SAS 1989–1996 Institute Inc., Cary, NC, USA).

Results

Nest occupation date, breeding success and nest size

Controlling for breeder age (older birds arrive earlier; GLMM: $F_{1,16} = 3.93$, estimate = –3.57, $p = 0.065$), larger nests were occupied significantly earlier than smaller ones (GLMM: $F_{1,16} = 3.93$, estimate = –0.01, $p = 0.037$). Pairs unable to lay eggs occupied smaller nests at the beginning of the breeding season (initial measure; GLIMMIX: $F_{1,105} = 13.07$, $p < 0.001$). Among pairs that laid eggs, clutch size was larger in bigger nests (GLMM: $F_{1,11} = 5.35$, estimate = 0.01, $p = 0.041$; Fig. 1) even accounting for the possible confounding effect of age (GLMM: $F_{1,11} = 5.26$, estimate = 0.12, $p = 0.042$; older individuals laid more eggs). Pairs breeding in nests of larger initial size showed a higher probability of fledging some chicks (GLIMMIX: $F_{1,66} = 5.18$, $p = 0.026$). Among these pairs successful in chick rearing — and accounting for the possible effect of age (GLMM: $F_{1,5} = 3.05$, estimate = 0.19, $p = 0.13$) — the total number of chicks fledged (productivity) was not related to nest size (GLMM, $F_{1,5} = 3.05$, $p = 0.14$) (but note the low power of these tests). Breeder age was not correlated with initial nest size ($F_{1,14} = 0.04$, $p = 0.85$).

Changes in nest size during the breeding season

Nest size increased during the breeding season (repeated-measures ANOVA: $F_{2,140} = 29.13$, $p < 0.001$; Fig. 2). The circularity assumption was not perfectly met, as epsilons showed some deviation from 1 ($\varepsilon_{GG} = 0.790$ and $\varepsilon_{HF} = 0.805$). Nevertheless, estimates of the F statistic according to the newly adjusted degrees of freedom showed that nest size increases were still highly significant (GG: df = 1.58, 112.27, $p < 0.001$; HF: df = 1.61, 114.40, $p < 0.001$). Nest size increase between the beginning of the breeding season and the end of laying was not significantly different from nest size increase between the end of laying and the end of the breeding season (paired t-test: $Z = 1.52$, $p = 0.12$, $n = 72$). Total nest size increase (from the beginning to the end of the breeding

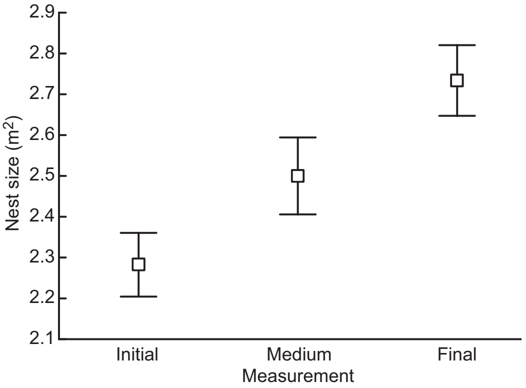

Fig. 2. Changes in nest size. The initial measure was taken prior to stork arrival (November), the medium measure just after the last egg was laid (April), and the final measure after chick fledging (July). Bars denote standard errors.

Fig. 3. Number of years occupied *versus* nest size. Nest size values are from the initial measure of 2008. The line represents the best fitted linear regression.

season) was not correlated with the initial size of the nest ($p = 0.32$), thus all nests increased similarly.

Changes in nest size and breeding success

Pairs unable to lay eggs showed smaller increases in nest size between arrival and the last week of April (*see* Nest size measurements section) than pairs successful in laying (increases between arrival and egg laying; GLIMMIX: $F_{1,96} = 14.94$, $p < 0.001$). Accounting for the confounding effect of breeder age (GLMM: $F_{1,18} = 1.20$, $p = 0.28$), nest size increase between arrival and egg laying did not predict clutch size (GLMM: $F_{1,18} = 1.68$, $p = 0.21$).

Nest size after laying increased more in nests that successfully fledged some chicks (GLIMMIX: $F_{1,84} = 7.05$, $p = 0.009$). However, such an increase was only marginally related to productivity (GLMM: $F_{1,13} = 4.34$, $p = 0.057$), again controlling for breeder age (GLMM: $F_{1,13} = 0.00$, $p = 0.99$).

Nest size increases between arrival and laying, between laying and fledging, or between arrival and fledging were not related to the age of breeders (all $p > 0.09$). Older, and thus more experienced and higher quality individuals did not carry more material than younger ones. To summarise, nest size increase during the breeding season depended only on the continuity of reproduction until the end of the season. The premature abandonment of nests by unsuccessful pairs implied the end of carrying material and consequently of nest growth. Among successful pairs, nest increase did not differ according to breeding success or breeder quality.

Nest size and number of occupation years

Nest size was significantly related to the number of years occupied ($r = 0.56$, $F_{1,143} = 65.83$, $p < 0.001$). Older nests were larger than recently built ones (Fig. 3). Interestingly, the annual growth rate of nests over the entire study period was almost the same as that recorded during a single breeding season (compare Figs. 2 and 3). This result suggests that nest size increases at a constant rate year-to-year.

Discussion

Nest size, sequential settlement and breeding success

In the present study, we found a strong relationship between occupation date and nest size in the white stork. In addition, we showed that individuals occupying larger nests are more successful breeders (e.g., higher clutch sizes and higher probabilities of laying and hatching), than those breeding in smaller nests. It is possible to hypothesize that the effect of nest size is purely a result of collinearity among individual age, breeding success and nest-site fidelity in this species (Vergara *et al*. 2006). In the white stork, age is a surrogate for individual quality or experience because older individuals have higher breeding success (Vergara *et al*. 2006, 2007b, Nevoux *et al*. 2008). Moreover, older (Barbraud & Barbraud 1999, Vergara *et al*. 2007b) or higher quality individuals (Kosicki *et al*. 2004, Tryjanowski *et al*. 2004, Tryjanowski & Sparks 2008, Fulin *et al*. 2009) also arrive earlier. Therefore, bigger nests would be occupied earlier in the season because older individuals return earlier to their previously used nests and reused nests are in fact the biggest. Furthermore, since older individuals have higher breeding success (Vergara *et al*. 2006, 2007b, Nevoux *et al*. 2008), higher breeding success in bigger nests would be another expected consequence. However, the association between nest size and both occupation date and breeding success prevailed in all cases, when the potential confounding effect of age was controlled for. Hence, individuals of the same age (and consequently similar arrival date and capacity to get a certain nest) occupy bigger nests whenever possible, and among birds from the same cohort those breeding in bigger nests achieve higher breeding success. Thus, our results suggest that big nests may be sought actively. Turn-over of individuals at the beginning of the breeding season (Wuczyński 2005, pers. obs.) and intense competition for nests observed in colonies of this species (Prieto 2002, pers. obs.) support this suggestion.

If we assume that individuals compete for bigger nests, the next step is to explore the reason for such selection. This may be possible if nest size provides benefits in terms of increased fitness. Several hypotheses have been proposed to explain the evolutionary mechanisms behind the fitness benefits of a large nest among bird species (Collias & Collias 1984, Fargallo *et al*. 2001, Soler *et al*. 2001). One hypothesis explaining the observed relationship between nest size and breeding success is that larger nests may be able to contain more fledglings than smaller ones. The white stork is a large species. Fledglings weigh around 3–4 kg and have a wingspan of around 1.5 m (Cramp & Simmons 1977). Before nest abandonment, chicks must exercise their wings and make some flying attempts. In a small nest, chicks are at greater risk of falling from the nest, which would have negative consequences both for the chick and the breeding success of their parents. Thus, nest size may restrict breeding success.

Another mechanism proposed to explain the relationship between nest size and breeding success in bird species is sexual selection. The nest could be an extended phenotype of individuals, since better nests (e.g., larger, more elaborate, more decorative, etc.) would accurately signal the quality of the builder (Fargallo *et al*. 2004, Tomás *et al*. 2006, Moreno *et al*. 2008). Therefore, individuals with better nests enhance the acquisition and/or the quality of their mate (Hoi *et al*. 1994, Evans & Burn 1996, Kleindorfer 2007, but *see* Pogány & Székely 2007). However, in nest reusers, nests are not likely to signal the quality of individuals as builders, since nests are already constructed in most cases. In these species, sexual selection may act by different mechanisms, such as defence capacity of the nesting-site against conspecifics. In the white stork, intense competition for nest occupation occurs because sites are strongly limited in colonies and individuals face absolute breeding failure if they are unable to get a nesting site. Therefore, a male able to acquire and defend a large nest would be signalling its high quality accurately and could mate with a higher quality female. The consequence of such nest competition would be a despotic distribution of individuals in the studied stork colony with the highest-quality individuals occupying the best nesting-sites. Indeed, older individuals (quality in the white stork is almost synonymous with age and experience) mainly occupy the centre of colony and the young ones the periphery, as has been demonstrated previously (Vergara & Aguirre 2006). However, a similar correlation between nest size and breeder age was not found in the present study. In addition, peripheral nests were not smaller than central nests (author's unpubl. data) as expected according to our previous work (Vergara & Aguirre 2006). One explanation for such results is that the possible role of nest size on nest selection and/or mate acquisition may be more important in younger (those breeding for the first times) than in older individuals, taking into account that this species shows a high rate of nest-site fidelity at older age-classes (Vergara *et al*. 2006). Moreover, the relationship between nest size and bird age could be non-linear due to senescence, i.e. the oldest and youngest birds could be relegated to the smallest nests. We do not, however, have sufficient data to properly test these hypotheses. Further studies would be necessary to understand this lack of relationship between breeder age and nest size and to elucidate the relevance of size restriction and/or parental quality on the association between nest size and breeding success in the white stork.

Is nest size an indicator of nest-site quality in the white stork?

Previous studies on the white stork have shown that nest quality (in terms of breeding success) is related to the age of the nest. The older the nest, the higher the number of fledglings (Sasvari *et al*. 1999, Tryjanowski *et al*. 2005). Our results support this finding in eastern populations of storks and suggest that the possible functional link between nest age and breeding success could be nest size. Given a long-term perspective, nest size may be a consequence of the quality of that nest site. Those nests located at the best nesting sites are occupied every year, every year some chicks are raised successfully, and consequently, their size increase steadily (*see* Fig. 3). However, small nests are signalling that they have been built recently or, in a long-term perspective, that their probability of breeding failure is high, since nests abandoned prematurely by unsuccessful pairs do not continue its size increase. Therefore, nest size may inform storks about the advantages of a certain nesting site in terms of ensured breeding success (e.g., low predation risk, low human disturbance, high stability of the structure, good microclimatic conditions for chick thermoregulation, etc.).

Several studies have revealed that nests located in better territories are occupied continuously or at least for a long time (Bocheński & Jerzak 2006) because they achieve higher breeding success (Nowakowski 2003, Tryjanowski *et al*. 2005, Denac 2006). The consequence of longer occupation is a bigger nest. For this reason, it has been hypothesized that nest size may be an indicator of breeding territory quality. However, this hypothesis does not hold for colonial populations because habitat quality and food resources in the surrounding areas are the same for all pairs (Bocheński & Jerzak 2006). For instance, in our study population, all individuals forage together in cattle meadows close to the nests and consequently all individuals have *a priori* the same opportunities to obtain the necessary food for their chicks. However, subtle differences in some environmental factors, such as slope or isolation, may affect breeding success between nests within colonies (De Neve *et al*. 2006). Therefore, if each nest site within a colony is related to some particular breeding conditions at the microscale, nest size may indicate nest quality within the colony in the case of the white stork. Future work analysing particular environmental factors at the microscale level (e.g. temperature, *see* Tortosa & Villafuerte 1999, Tortosa & Castro 2003) at each nest may help in understanding the link between nest size and breeding success in colonies of this species.

Nest-building behaviour during the nesting phase

White stork individuals carry material to the nest throughout the breeding season (Schulz 1998), but, to the best of our knowledge, no previous study has assessed such behaviour. We found a relationship between the amount of material carried to the nest and the probability of hatching and fledging chicks. Rather than a causal link between breeding success and material carried, this relationship is probably showing a link between the length of nest occupation and nest size. Nest growth ceases when reproduction fails and the nest is abandoned. However, the nest keeps growing while nesting occurs. Therefore, nests that increased the most in size were those occupied the longest. The amount of carried material prior to and after egg laying in successful pairs was similar, suggesting that nest building behaviour is permanent and, to some extent, independent of the breeding stage.

White stork nest building behaviour could have several functions. Previous studies have shown that individuals adjust their reproductive effort according to post-mating behaviour of their mates (Moreno *et al*. 1994, Soler *et al*. 1998a, 1998b, De Neve & Soler 2002, De Neve *et al*. 2004, Martínez-De la Puente *et al*. 2009). The continued nest-building behaviour of the white stork could be a post-mating signal. Nest-building behaviour is costly, and only individuals in good condition might be able to carry new material to the nest (Fargallo *et al*. 2001, Tomás *et al*. 2006). However, our results do not support this hypothesis. Breeder age, an index of individual quality in this species (Barbraud & Barbraud 1999, Vergara & Aguirre 2006, Vergara *et al*. 2006, 2007b, Nevoux *et al*. 2008), was not significantly related to the amount of material added to the nest. Other parameters of individual quality, such as clutch size or productivity, were not related to nest size increase either. Therefore, females did not lay larger clutches in response to males that are more active in nest building, neither do individuals enlarge their nests more if broods are larger to indicate their parental care abilities to their mates. Nest growth seems to be a matter of continuity in reproduction. Nevertheless, other potential confounding variables, such as parental care by each sex, other nest traits (e.g., density, *see* Quesada 2007), or type of material carried to the nest, were not assessed in the present study.

White stork chicks suffer from high mortality at younger stages due to their low capacity for endothermy (Carrascal *et al*. 1993, Tortosa & Castro 2003, Jovani & Tella 2004). It has been demonstrated that adults carry dung during the early phases of nestling development to maintain nest temperature (Tortosa & Villafuerte 1999). The observation of nest size increase after laying date would agree with this hypothesis. Nevertheless, thermoregulation as a function of nest size would only be valid if material is carried to the nest during the earliest phases of nestling development. We are, however, unable to evaluate this hypothesis because the final measurements of nests were carried out after fledging. Future studies could address this issue by making extra observations after the hatching date.

Finally, another possible and non-excluding hypothesis explaining nest building behaviour after mating in the white stork is maintenance. Stork nests are solid constructions but they are open and completely subjected to degradation by rainfall, wind, or snow. Taking into account that nests are reused for many years, the necessity of repairing activity against weather effects is clear. Even over a period of a few months (a single breeding season), the deterioration of unoccupied or abandoned nests is obvious (pers. obs.). Moreover, fledgling and adult activity in the nest wears down nest structure. Therefore, the continued contribution of new material counterbalances degradation of the nest. In addition, high nest-site fidelity by this species (Barbraud *et al*. 1999), which is especially marked after successful breeding attempts (Vergara *et al*. 2006), may explain why adults continue their nest-building behaviour even after chicks have fledged.

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